INHERITANCE IN A DIALLEL CROSSING EXPERIMENT WITH LONGLEAF PINE

E. B. SNYDER
GENE NAMKOONG

Southern
Forest
Experiment
Station

Summary

Seven-year-old progeny from crosses among 13 randomly selected parent trees provided genetic information on 51 growth, form, foliage, branch, bud, and pest resistance traits. Presented are heritabilities, phenotypic and genotypic variances, covariances, General Combining Ability (GCA), Specific Combining Ability (SCA), and environmental correlations for all measured traits. The results were compared to those from wind pollinations and to parent-tree measurements where appropriate.

There were significant GCA effects for 35 and significant SCA effects for 25 of the traits; the latter were small and unimportant by comparison. There were almost no maternal, reciprocal, or genetic x environmental (GxE) effects.

Parent-progeny correlation coefficients for traits ranged from 0.0 to 0.9 and were generally proportional to the sib-heritabilities. High genetic correlation between 3-year and 7-year heights further suggests a trend toward a juvenile-mature relation high enough to justify selection of families soon after emergence from the grass stage. This procedure would permit short-term progeny testing of ortets before clonal orchards are installed.

GCA correlations between control- and open-pollinated (OP) families were proportional to sib-heritability values, indicating that wind-pollinated seed resulted in efficient progeny tests. Estimates of GCA variances from OP's were generally larger than those from crosses.

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Introduction

Longleaf pine (*Pinus palustris* Mill.), traditionally the premier southern pine for wood quality, is regaining interest among tree planters because it is the best adapted species for many sites. If this interest is to continue, genetic solutions must be found to some of the problems which have limited its acceptance in planting programs during the past half century. Low average growth rate due in part to delayed juvenile stem elongation is perhaps the most serious and has tended to limit efforts to develop faster growing strains of the species.

Much breeding progress is being made through propagation by scions and progeny of selected superior or elite trees. Experience in breeding of other plants suggests, however, that after a few plant generations, a plateau is reached from which further gains require basic knowledge of species-specific trait inheritance patterns. That this need will arise in the improvement of forest trees is almost a certainty. Among the other southern pines, some degree of common applicability of basic knowledge may be expected, and results of some studies of this kind are available. Longleaf pine, with its unique juvenile traits, is unlikely to share much of this background, so basic studies of this species are essential to its optimum genetic improvement.

Because both tree breeding programs and tree genetics studies are expensive operations, requiring long periods of time, it is highly desirable that both types of efforts be conducted simultaneously. In recognition of this need, the study on which this report is based was designed and initiated more than 20 years ago. This study is unique for longleaf pine in its design for obtaining basic data on interrelationships of a wide spectrum of traits. Many of these were pictorially presented by Stephenson and Snyder (1969) and include height, volume, survival, branching, foliage, bud characteristics, and pest resistance.

Breeding of this species, as for other pines, emphasizes rates of fiber production—development of genetic strains that are efficient producers of cellulose. While simply expressed in terms of wood volume per unit of time, such efficiency is dependent upon a complex of probably inherited traits related to the efficiency of photosynthesis. Among these are morphological traits of needles and branches that affect exchanges of water and gases and exposure of chlorophyll to radiation. Exploration of the genetic relationships of such factors and their physiological impacts could provide effective breeding alternatives in the development of efficient longleaf pine trees—alternatives of particular importance in view of shifts in wood utilization objectives brought about by the harvest of increasingly smaller trees. Similarly, many traits little used in current tree breeding may prove useful as easily measured indicators of closely related traits, or may contribute to location of specific genes on certain chromosomes. To extract maximum possible values, therefore, from the heavy investments of time, land, and manpower in this study, analyses were made on as many gross morphological traits as feasible.

In addition to its multiplicity of analyzed traits, this study was designed to evaluate inheritance in a random sample of a population, rather than in parents selected as superior phenotypes, as is the case with many other genetic studies. Random selection of parents is essential to achieve our objectives, which are based on the general genetic statistical concept of random, normally distrib-

E. B. Snyder and Gene Namkoong are Principal Plant Geneticists, Forest Service—USDA. Snyder is with the Southern Forest Experiment Station, Gulfport, Miss. and Namkoong is with the Southeastern Forest Experiment Station, Raleigh, N.C.

uted populations. In effect, the findings of a random sample can be expected to apply to other similarly selected samples of the same populations. Analyses of data from selected parents, on the other hand, apply only to the trees studied, and their applicability to other groups of trees is questionable.

Study of variations among families derived by interbreeding randomly selected parent trees from a longleaf pine population can provide information basic to the understanding of the genetics of the species and to rational methods for its improvement. Relative magnitude of additive and dominance variance, measured respectively by general and specific combining ability variances, largely determines the choice between single population and hybrid breeding methods. Maternal and reciprocal effects, and the effects of genotypic interactions with environment can affect the efficiency of testing. Sizes of these variations, and of that due to unexplained error, thus affect the choice of both the most responsive traits and the selection method.

To provide these types of basic information, randomly selected trees from a longleaf pine population in Mississippi were intercrossed in a complete diallel mating pattern; open-pollinated seed was also collected from the same parent trees. Data on the parents and derived families provide the bases for the analyses in this paper.

Specific objectives of the study are to:

1. Evaluate parent-progeny relations and thus determine the effectiveness of parental selection and juvenile selection among progeny families.

2. Compare controlled crosses and open pollination for estimating variances and evaluating individual parent general combining abilities.

3. Estimate relative importance of genetic and nongenetic sources of variance.

4. Estimate the covariances and correlations which exist among traits, the sizes of the various genetic and nongenetic sources of the correlations, and the correlated responses which can occur if selection for one trait also affects another trait.

5. Evaluate the usefulness of various traits or sets of traits for breeding or quantitative genetic study, any special requirements for their testing, and their utility as constituent or composite traits.

Materials and Methods

Parent Tree Sampling and the Crossing Scheme

In 1956, 13 open-grown longleaf pine trees aged 19 to 29 years were randomly selected from a large,

more or less continuous population near Gulfport, Mississippi, and were intercrossed in all combinations. The distance of one selected tree from another varied from 43 to 1172 ft (13 to 357 m). The nature of the stand is illustrated in figure 1.

Pollinations in 1956 and 1957 produced seed for eight replications of all 78 combinations of a complete half diallel, excluding selfs. In addition, there was sufficient seed from reciprocal pollinations in 69 of the crosses for installation of at least two replications. Thus, there were 147 of the 169 (13 x 13) possible control-pollinated families. All parents yielded sufficient open-pollinated seed for eight complete replications. While 11 of the parents yielded self-pollinated seed, the amounts are too small to have quantitative genetic pertinence; tests of these seeds will be reported elsewhere.

Planting and Measuring

Progeny from the selected parents were outplanted in four replications at each of two locations 2 miles (3.2 km) apart. Within replications full-sib and open-pollinated families were randomly assigned to eight-tree row plots. Where seedlings of reciprocal crosses were available, plots were divided into two four-tree subplots, one planted with seedlings from the cross and the other with

Figure 1.—*Parent 10 in 1958.*

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progeny of the reciprocal cross. Where this was not feasible, eight trees from identical crossings were planted.

Seed from 1956 pollinations was stored and combined with that pollinated in 1957 for germination in the spring of 1960. Outplanting was on typical longleaf pine sites, which had been bulldozed, plowed, and disked. The experiment was planted with 1-year-old nursery stock grown in milk carton pots (Smith and others 1963). First-year survival averaged 94 percent. Trees were spaced 12 ft (3.7 m) apart, at the apexes of equilateral triangles. After planting, the site was well cultivated for 2 years and thereafter mowed periodically. It was sprayed with Bordeaux mixture three times a year for the first 3 years.

Parent trees were measured for growth and branch traits in 1957. The branch measurements were made by climbing the trees and measuring two to seven whorls in the central crown as recommended by Snyder (1961). Parent bud lengths and diameters were measured February 4, 1966, and bud lengths again on March 4, 1966. Needle and bud scale traits were measured in November 1966 and again in July 1967. In the parent-progeny computations, parent measurements of the two dates were averaged, except for bud scale length which was based only on the November measurement.

In the plantations, 3-year height (trait 49) was recorded in the spring of 1963, 5-year height (trait 1) early in 1965, and 27 other traits in 1967 (table 1). The latter measurements were on 7-year-old trees, but bud, branch, bole section, and needle measurements were restricted to branches which had started development the fifth year. The length and diameter of a bole section between the fifth-year and sixth-year whorls were measured in addition to total tree height and d.b.h. Branch sampling was restricted to the fifth-year whorl. Needle traits were measured on that part of a single branch covered by the most recent mature needles, bud traits on the main bud of the same branch. This type of sample progressed by replication over a 4-month summer period. Needle droop angle was determined as the average degree deviation of the needle bundle from horizontal when supported horizontally by its basal (sheathed) portion.

Trait Construction and Contributions of Constituent Traits

From the 29 original measurements of progeny, 51 were developed for analysis, some of which were unaltered original measurements or transformations thereof, and others were combinations of the original data with or without transformations (table 1). Biological interpretations of transformed data were found to be the same as those for original data. In addition to these 51 traits, information on bud cortical oleoresin is available from past work (Franklin and Snyder 1971).

From a small sample of cross-sectional drawings of needles, we determined that perimeters could be derived as widths x 2.5 and dorsal arcs as widths x 1.3.

The bole section taper factor was computed as $(1/2 + a^2/2b^2)$, where b is the basal diameter (above fifth-year whorl) and a is the apical diameter (below the sixth-year whorl). This factor is proportional to the ratio between the midsection area and the area of the basal section,

$$\frac{a^2 + b^2}{8} \div \frac{b^2}{4}$$

Thus, as taper factor approaches unity, the bole section form, assumed to be a truncated paraboloid, approaches that of a cylinder, i.e., the larger the factor, the less the taper.

Data were transformed as indicated in table 1 for the following reasons:

1. Branch length data (trait 46) were transformed to square roots to scale the traits more additively, i.e., to make progeny and parental values correspond more closely (Mather 1949).

2. For data taken as proportions, the Freeman-Tukey arc sine $\sqrt{\text{percent}}$ transformation (Mosteller and Youtz 1961) was used to achieve homogeneity of error variances. An exception is 7-year survival, which was transformed to logarithms to conform to its use in combining traits as discussed below.

3. Simple ratios involving logarithms were constructed for six of the traits. In these cases, the two traits making up the ratio are assumed to be in a linear functional relationship in their transformed scale such that a reduction in one component induces a proportionate reduction in the other component (e.g., $Y = bx$, or $b = Y/x$). Differences between ratios are then considered as indicating differences in the proportionality. The analysis by logs is intended to indicate which genetic or environmental sources of variance cause differences in that proportionality factor. Alternatively, the ratio analyzes the trait in the numerator independently from changes measured by the trait in the denominator.

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Figure 1.—*Parent 10 in 1958.*

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Table 1.—*Traits of study progeny analyzed. Except where otherwise noted, traits were evaluated in 1967, when trees were 7-years old*

	Trait Number and name	Measurement or derivation details	Units as analyzed
1	5-year height	Measured, spring 1965	ft
2	March bud length	On three 5th year branches	cm
3	Bud scale length	On one 5th year branch; see trait 25	mm
4	Bud scale width	On one 5th year branch	mm
8	Branch angle (at attachment)	On all 5th year branches; see trait 31	degree
9	Needle number/branch	$100 \times$ (total weight of needles on one 5th year branch)/(green weight of 100 needles) on same branch: see trait 36	number
10	Needle weight/branch	On one 5th year branch, weighed green	g
12	3-year height, (trees >1 ft)	Trees <1 ft tall excluded, compare trait 49	ft
13	Height growth (3rd to 5th yr)	Increment	ft
14	Height growth (5th to 7th yr)	Increment	ft
15	7-year height		log in
16	7-year basal area	At 7 years, from d.b.h.; 3 added to avoid negative logs	$\log \text{in}^2 + 3$
17	7-year tree volume	Traits 15+16; proportional to individual tree volume	$\log \text{in}^3 + 3$
18	Length (bole section)	5th to 6th whorl	log in
19	Basal area (bole section)	From diameter of bole section at 5th whorl	$\log \text{in}^2 + 3$
20	Bole section taper factor	Ratio of midsection to basal area, see text	log ratio
21	Volume (bole section)	Traits 18+19+20	$\log \text{in}^3 + 3$
22	January bud length	On three 5th year branches	cm
23	Bud length growth	Growth from January to March, traits 2-22	cm
24	Bud diameter	On three 5th year branches, March	mm
25	Bud scale length, adjusted	On branch; allometrically adjusted for width, see text	log mm
26	Branch length/tree ht. ratio	Mean of all 5th year branches/(7 yr height)	log ratio +1
27	Branch/bole mid-diam² ratio	(Mean of mid-diameters of all 5th year branches)²/(mid-diameter of bole section)²	log ratio +1
28	Number of 5th year branches	All branches initiated 5th year	log number
29	Branch/bole volume ratio	(Mean of all initiated 5th year)/bole volume; traits 26+27+28−17	log ratio +2
30	Branch angle (average)	All 5th year branches, except last growth flush	degree
31	Branch angle (attachment)	All 5th year branches; see trait 8	log cosec
32	Branch/bole diam² ratio	(Mean branch basal diameter of 5th year branches)²/(bole section basal diameter)²	log ratio
33	Knot area/bole diam² ratio	(Knot area)/(bole section basal diameter)²; traits 31 + 32	log ratio
34	Needle length	On three needles from one 5th year branch	log cm
35	Needle perimeter	On three needles from one 5th year branch; width × 2.5	log cm +2
36	Needles/branch	On one 5th year branch; see trait 9	log number
37	Foliage surface	On all 5th year branches, traits 28+34+35+36	$\log \text{cm}^2 + 2$
38	Weight/needle	Trait 10 − trait 9	log g + 1
39	Foliage weight	On all 5th year branches, traits 28+36+38	log g + 1
40	Adjusted foliage surface	Trait 37 allometrically adjusted by trait 21, volume; see text	$\log \text{cm}^2$
41	Adjusted foliage weight	Trait 39 allometrically adjusted by trait 21, volume; see text	log g
42	Stomate rows/cm of arc	Rows/(cm of dorsal arc) where dorsal arc = width × 1.3	log number
43	Stomates/cm of row	Number/cm of row on dorsal surface of three needles	log number
44	Stomate density	Number/cm² of dorsal surface; traits 42 + 43	log number

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Table 1.— *Traits of study progeny analyzed. Except where otherwise noted, traits were evaluated in 1967, when trees were 7-years old*

Trait		Measurement or derivation details	Units as analyzed
Number	and name		
45	Needle droop	On three needles; deviation from direction of sheathed base of needle; see text	degree
46	Branch length	All 5th year branches	ft$^{0.5}$
47	Branch needle persistence	Percent of length of 5th year branches retaining needles	arc sine $\sqrt{pct}$
48	Stem needle persistence	Percent of bole length retaining needles	arc sine $\sqrt{pct}$
49	3-year height (all trees)	Trees <1 ft included; compare trait 12	ft
50	7-year survival	Percent of trees in plot or subplot alive	log pct + 2
51	Volume (plot)	Traits 15+16+50	log in^3 + 5
52	Volume (plot, bole section)	Traits 18+19+20+50	log in^3 + 5
57	Trees forking	Percent of plot trees forked	arc sine $\sqrt{pct}$
58	Trees >1 ft at 3 years	Percent of plot trees >1 ft high at 3 years	arc sine $\sqrt{pct}$
59	Trees with fusiform rust	Percent of plot trees with fusiform rust	arc sine $\sqrt{pct}$

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4. For traits 25, 40, and 41, a function $Y = bx^k$, known as the allometric relationship was used. Differences in proportionality due to one trait's changing faster than the other can be tested. When k is one, the ratio has the same properties as the simple ratio above. Conversion to the logarithmic scale allows a general assumption of linearity and the use of linear least square-regression techniques (Baskerville 1972). An overall experimental estimate of constants in the formula was computed from plot means. The deviation of each tree or plot value from that expected according to the formula was then computed as a measure of variation for the trait in question independent of allometric growth.

5. For each of the remaining traits, a 5-percent sample of data was checked to determine if the within-plot variances were independent of the means (Box and Cox 1964). Transformation to logarithms adequately removed scale effects and provided more homogeneous error variance distributions for traits whose variance was not independent.

Many traits were derived by combining simpler ones, i.e., two or more constituent traits were combined into a composite trait by some functional relationship such as multiplying them together (Pritchard and others 1973). Additivity is regained in such cases by expressing measurements in logarithms. For example $\log_{10}$ tree volume (trait 17) can be expressed as: log volume = log height + log basal area.

The variance of a composite trait equals the sum of the variances of constituent traits plus twice the sum of covariances. Because its contribution to covariance cannot be computed (Griffing 1953), the relative contribution of a constituent trait cannot be determined. Where traits are linearly related, however, the contribution of each is within the following limits: (a) its variance (if it contributes nothing to covariance) and (b) its variance plus two times the sum of its covariances (if it should be responsibile for all of its covariances).

In this study we separately analyze the composite traits and compare results with the genetic and other sources of variance derived from the sum of constituent variances and covariances. This approach is desirable because analysis of only the constituent traits does not afford an accurate estimate of the variances of a complex trait whose constituents are not completely independent of each other or are not related to each other and the composite trait in a simple linear manner.

If a composite trait has a larger heritability than any of its constituents, we conclude that it, as well as its constituents, is useful in evaluating potential gains.

Although foresters have often evaluated the relative worth of constituent traits according to their contribution to the mean or variance of the composite trait, use of a selection index unweighted for economic value affords superior genetic information. The relative importance of any constituent trait in such a selection index is measured by the percent reduction in rate of genetic gain in the composite trait when the constituent is dropped from the index (Cunningham and others, 1970). Thus, the magnitude and relationships of heritability, phenotypic correlations, and genetic correlations are simplified into a single percentage reduction value—a value considerably more appropriate in evaluating the importance of a trait in breeding than any one of the three parameters separately. The percentage genetic contribution of each constituent trait was computed in this manner.

Assumptions and Analyses—Crosses

The assumptions for the analyses of variance and the genetic variance expectations of the components of variance are the usual ones for non-related, random parents from a diploid population (Cockerham 1963). The genetic model and analysis method are given by Schaffer and Usanis (1969). Effects accounted for with degrees of freedom (df) adjusted for missing families are:

Source	df	Expected Mean Squares
Locations	1	
Replications/ Location	6	
General Combining Ability (GCA)	12	$\sigma^2 + C_5 \sigma^2_{gxl} + C_9 \sigma^2_r + C_{12} \sigma^2_m + C_{14} \sigma^2_{sca} + C_{15} \sigma^2_{gca}$
Specific Combining Ability (SCA)	65	$\sigma^2 + C_4 \sigma^2_{gxl} + C_8 \sigma^2_r + C_{11} \sigma^2_m + C_{15} \sigma^2_{sca}$
Maternal Effects	12	$\sigma^2 + C_3 \sigma^2_{gxl} + C_7 \sigma^2_r + C_{10} \sigma^2_m$
Reciprocal Effects	56	$\sigma^2 + C_3 \sigma^2_{gxl} + C_6 \sigma^2_r$
GCA x Location	12	$\sigma^2 + C_1 \sigma^2_{gxl}$
Error	839	σ^2

The design is unbalanced because of missing families and plots. However, the analytical procedure sequentially fits the mean squares; hence, the expected values of the mean squares contain unequal "c" coefficients. The effects were fitted in the sequence given in the above table. Analyses of covariance were also performed by the same analytical procedures. Here the coefficient set is the same as for the variance analyses which contained the minimum set of entries.

We computed complete analyses of variance and covariance according to Method 3, Model 2 (Griffing 1956, Cockerham 1963), i.e., effects are all random and matings include crosses and reciprocals but not selfs. The degrees of freedom and sums of squares are adjusted for missing families and plots. The analysis includes terms for maternal and reciprocal effect and the interaction of General Combining Ability with location (GxE). We also computed the expectations of mean squares all variance components, and their standard errors (SE's).

The analytical strategy was to remove from vital treatment and error mean squares as many inflationary effects from the linear model of effects as allowed by the capacity of the computer (Namkoong and others 1966). A preliminary sample of a few characters was first run. For this sample, data were selected so that all reciprocals were present in all replications. Since the reciprocal and maternal effects were generally negligible and since effects of their interaction with location would also be negligible, such effects were subsequently included with error variance.

Limited computer capacity prevented separating out the specific combining ability × location effect; we pooled this into error without test. Subsequent analyses showed that for this particular experiment the General Combining Ability × location effects were never significant; the interaction of the usually smaller Specific Combining Ability × location effects would thus not bias the error appreciably.

Plot mean data were used as the units of analysis. However, it is often necessary to express heritabilities on an individual tree basis. Hence, estimates of tree variation within plots are needed. A separate program was used to segregate among- and within-plot sources of variation:

Sources of variation	df
Plots	1003
Within plots	2459
Total (individual)	3462

Since the within-plot MS estimates σ_w^2, error MS expectation for plot means is:

$$\sigma_e^2 = \sigma_p^2 + \sigma_w^2/k \text{ or } \sigma_p^2 = \sigma_e^2 - \sigma_w^2/k \text{ where } \sigma_p^2$$

= variance among plots and k = harmonic mean of number of trees per plot.

Some trees had no branches and hence lacked values for certain traits. This lack posed a problem since there were 3946 trees measured for at least some traits but only 3340 for all traits. If all the trees on any plot were devoid of a certain trait, the plot was omitted for all traits.

This experiment is based on the premise of a random selection of parents with the variation among their progeny means being adequately described by variance components of the sample of progeny. In such situations, one is not generally interested in examining the performance of the progeny of individual parents. General Combining Abilities were computed, however, for each parent from the crossed progeny and from the open-pollinated progeny because they were needed in computations supplementary to those in DIALL. To attain these values, two computer programs were developed and used. First, family means were derived by a missing plot randomized complete block program. The means were then entered into a least squares program (Snyder 1975), and the GCA's were extracted.

Negative components of variance were handled as recommended by Thompson and Moore (1963), i.e., a mean square smaller than a predecessor mean square and whose component is included in it is pooled with the predecessor and the result equated to both expectations.

Where individual trees were the basis of measurement, heritability (h^2) estimates were calculated by the formula:

$$h^2 = \frac{4\sigma_{GCA}^2}{\text{Phenotypic variance}}, \text{ where the phenotypic}$$

variance = $\sigma_{GCA}^2 + \sigma_{SCA}^2 + \sigma_{Mat.}^2 + \sigma_{Recip.}^2 +$

$\sigma_{GxL}^2 + \sigma_{Plot}^2 + \sigma_{Within plot}^2$

When the measurement was by plot, as for survival, forking, etc., heritability was computed as:

$$h^2 = \frac{\sigma_{GCA}^2}{\text{Phenotypic variance}}, \text{ where the phenotypic}$$

variance = $\sigma_{GCA}^2 + \sigma_{SCA}^2 + \sigma_{Mat.}^2 + \sigma_{Recip.}^2 +$

$\sigma_{GxL}^2 + \sigma_e^2.$

Heritability was also calculated for families on a replicated plot basis, i.e., as if there were eight replications of four trees each. This is an arbitrary assignment which is not meant to reflect the structure for any particular experiment but is convenient and appropriate for experiments similar to ours. Here the respective denominators are for individual tree traits:

$$\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat.} + \sigma^2_{Recip.} + \sigma^2_{GxL} + \sigma^2_{Plot/8}$$
$$+ \sigma^2_{Within/32}$$

or for plot characters:

$$\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{Mat.} + \sigma^2_{Recip.} + \sigma^2_{GxL} + \sigma^2_{e/8}.$$

To compute the percentage of genetic gain (G), the standard formula (Falconer 1960) was used except that i, the selection intensity, was taken as 2i because both parents would be selected. For traits analyzed as logarithms, the gain formula is used in the log units. Thus, ΔG (logs) $= \log \overline{X}_1 - \log \overline{X}_o$, where $\overline{X}_1$ represents the mean of the selected population and $\overline{X}_o$ that of the original population. Since the ratio of logs does not equal the log of the ratio, a computation is necessary to express gain after retransformation as a comparable ratio in original units. To do this, we consider that we want to obtain an expression of:

$$\frac{\Delta G \text{ (original units)}}{\overline{X}_o} = \frac{\overline{X}_1 - \overline{X}_o}{\overline{X}_o}$$

Since we assume that it is appropriate to estimate gain in log units, then:

$$\Delta G \text{ (logs)} = \text{Log } \overline{X}_1 - \text{Log } \overline{X}_o$$

$$= \text{Log } (\overline{X}_1/\overline{X}_o),$$

and hence, anti-log ΔG (logs) $= \overline{X}_1/\overline{X}_o$.

$$\text{Then, } \overline{X}_1 = \overline{X}_o \text{ [anti-log } \Delta G \text{ (logs)]},$$
$$\overline{X}_1 - \overline{X}_o = \overline{X}_o \text{ [anti-log } \Delta G \text{ (log)} -1],$$
$$\text{and Gain} = \frac{\overline{X}_1 - \overline{X}_o}{\overline{X}_o} = \frac{\Delta G}{\overline{X}_o} \text{ (original units)} = \text{anti-log } \Delta G \text{ (logs)} -1$$

We use such an estimate because it corresponds better to the original scale than does the log scale.

Several correlations, components of the total phenotypic correlation, are reported: those of the GCA effects, the SCA effects and the environ-mental effects. Our estimate of the correlations is the ratio of the covariance of two traits to the geometric mean of the respective variances. Total variances, covariances, and phenotypic correlations were obtained by computer program CORREL (Cooley and Lohnes 1962). Text discussions arbitrarily relate mainly to those GCA correlations which equaled or exceeded 0.70.

Because of the missing plots, significance of variance components can be judged more easily by the ratio of the component to its standard error than by a constructed F-test. Any component of variance more than twice its standard error is arbitrarily judged to be greater than zero. The t-test for regression coefficients was used to determine significance of parent-progeny regression coefficients. The error variance used for this test is derived from the deviation from regression. All tests of significance were made at the 0.05 level of probability.

Assumptions and Analyses — Open-Pollinations

Analyses of variance on the open-pollination (OP) data had the following form:

Plot data		Individual tree data	
Source of variation	df	Source of variation	df
Replications	7	Plots (total)	103
Families	12	Within plot	484
Error	84		

The σ^2_f values were extracted in the standard manner and their significance determined by the F-test (MS families/MS error). General Combining Ability values and variances were calculated for comparison with those from controlled cross estimates (Snyder 1975).

Results

The estimates and evaluations we list as objectives are necessarily trait-dependent. Some generalizations can be made, however, about a number of relationships and sources of variance before presenting detailed findings for specific traits.

Parent-Progeny Relations

Parental values for 18 traits were measured or derived. Each of these traits was analogous to a similarly numbered trait analyzed for the progeny. Parent phenotypic values for each trait were regressed on General Combining Ability values derived from the progenies. Results are presented in table 2, in order of decreasing coefficients of

Table 2. — *Parent, progeny means, variances, correlation statistics and sib-heritabilities, age 7*

	Trait	Mean		Variance		Covariance	b	r	Sib-heritability h^2 plot basis
		Parent	Progeny	Parent	Progeny				
24	Bud diameter (mm)	10.4	9.9	0.383	0.048	0.116	0.31*[1]	0.86	0.83
43	Stomates/cm row (log number)	2.05	2.01	.00774	.00091	.00213	.28*	.80	.65
3	Bud scale length (mm)	21.5	16.5	48.28	5.30	11.84	.25*	.74	.49
38	Weight/needle (log g + 1)	.486	.421	.0550	.0052	.0118	.22*	.70	.53
42	Stomate rows/cm of arc (log number)	1.68	1.68	.0278	.0019	.0050	.18*	.70	.75
35	Needle perimeter (log cm + 2)	1.64	1.58	.00734	.00075	.00159	.22*	.68	.55
27	Branch/bole mid-diam^2 ratio (log + 1)	-.042	-.127	.0593	.0038	.0094	.16*	.62	.14
4	Bud scale width (mm)	3.54	3.30	1.232	.086	.200	.16*	.61	.29
34	Needle length (log cm)	1.48	1.54	.00717	.00137	.00190	.26*	.61	.50
31	Branch angle, (attachment) (log cosec)	.0359	.0390	.00399	.00034	.00070	.18*	.59	.59
22	January bud length (cm)	4.78	4.30	4.18	1.35	1.34	.32*	.56	.71
45	Needle droop (dg)	21.3	28.0	342.0	49.8	69.5	.20*	.53	.53
15	Annual ht growth x 7 (log in)^2	2.28	2.39	.0299	.0020	.0034	.11	.43	.25
9	Needles/branch (number)	496	999	96800	25000	17400	.18	.34	.43
23	Bud length growth (cm)	1.14	0.83	1.731	.172	.178	.10	.32	.36
20	Bole section taper factor (log ratio)^2	-.107	-.086	.00403	.00024	.00031	.08	.31	.28
26	Branch length/tree ht ratio (log + 1)[4]	.174	.912	.0418	.0104	.0034	.08	.16	.40
16	Annual basal area x 7 $\frac{(\log \text{in}^2 + 3)^2}{}$	3.82	3.89	.121	.006	-.001	.00	-.03	.18

[1]Asterisk indicates rejection of null hypothesis at 0.05 level
[2]Seven years of growth used as basis, i.e., 23 years of parental growth reduced to 7-year basis
[3]Parental taper calculated from first log; progeny taper from fifth-year bole section
[4]Parental divisor was diameter instead of height as for progeny because it gave better size correction

correlation (r). In the absence of nonadditive genetic effects, b values would approach $h^2/2$, and, in the absence of error variations, r values would approach 1.0 if parent and progeny variances were equal. To approximate such ideal results, measurements would have to be refined, parents replicated by cloning, progeny well replicated, and the traits controlled by the same genes in the parents as in the progeny.

Test results (table 2) indicate general agreement between the parent-progeny correlations and the heritabilities developed from progeny variances. Among 18 traits, those with high heritabilities tended to have higher b and r values. This finding confirms that in these cases trait variations that were strongly inherited corresponded to measured morphological variations in the parents. Thus, selection of parents for such morphological traits can result in genetic gain. Also, as early as age 7, progeny exhibit traits that can be measured in mature (25-year) parent trees; we see nothing to prevent them continuing to show these trait variations to and beyond the age at which the parents were evaluated.

Maternal, Reciprocal, GxE, and SCA Effects

One of the more surprising results of this study was the almost complete lack of significant maternal and reciprocal effects. In marked contrast, many GCA and SCA effects, estimated with approximately the same or fewer degrees of freedom and larger error, proved significant. While other handling procedures or sites might affect results, we feel that our conditions were reasonably representative. The lack of maternal and reciprocal effects indicates that under similar conditions future experimentation with longleaf pine can safely ignore possible biases from these sources. Thus, progeny tests and variance estimates of juvenile growth and form can be safely made without regard for maternal effect biases. Significant $G \times E$ interactions were similarly lacking for all traits, but because our test sites varied little, more extensive testing of genotypes and environments is needed.

Of the 51 traits, 51 percent had significant SCA effects (table 3), and 69 percent had significant GCA effects. The frequency of significant SCA effects is large in view of the rarity of published reports of such effects. Their relative sizes, however, when expressed as ratios comparable to heritability ratios do not exceed 0.16. For such slight gains, the higher costs of utilizing non-

Table 3. — *The magnitude of significant Specific Combining Ability (SCA) effects*

	Trait	$4 \sigma^2_{SCA}$ Phenotypic variance
1	5-year height	0.10
13	Height growth (3rd to 5th year)	.14
15	7-year height	.16
16	7-year basal area	.15
17	7-year tree volume	.16
51	Plot volume	.08[1]
18	Length (bole section)	.07
19	Basal area (bole section)	.13
21	Volume (bole section)	.13
52	Plot volume (bole section)	.06[1]
28	Number of 5th year branches	.15
41	Adjusted foliage weight	.09
34	Needle length	.11
35	Needle perimeter	.06
38	Weight/needle	.08
48	Stem needle persistence	.09
27	Branch/bole mid-diam² ratio	.12
29	Branch/bole volume ratio	.07
46	Branch length	.10
8	Branch angle at attachment (degrees)	.08
31	Branch angle at attachment (log cosec)	.08
32	Branch/bole diam² ratio	.08
33	Knot area/bole diam² ratio	.09
59	Trees with fusiform rust	.05[1]
22	January bud length	.04

[1] $\dfrac{\sigma^2_{SCA}}{\text{Phenotypic variance}}$ for these plot values.

additive variance (SCA) are unlikely to be justified in longleaf pine breeding while additive variances remain to be exploited.

Results of Cross- and Open-Pollinations

Breeders frequently calculate heritabilities from open-pollinated (OP) progeny tests. Kraus (1971) hypothesized that parents could be inexpensively and efficiently ranked by such tests. We compared, for all traits, both variance components and rankings from OP progeny with those from controlled crosses.

The GCA components from OP progeny averaged twice that from crosses, except that for traits 9, 18, 34, 35, and 38, they were 0.4 to 0.7 as large. Except for trait 28, number of branches, these traits relate to needles. The following sources of error can bias this comparison: the number of

effective male parents in the OP families for some females may be very limited, the SCA effects may be large, and the error variances for the two kinds of family plots may differ. A very restricted number of effective males affects the estimates of σ^2_{GCA} and σ^2_{SCA} since single males make the difference between family averages more like full-sib differences and would confound GCA and SCA effects in the σ^2_{GCA} estimates. Thus, the variance among OP families would not be the variance among half-sibs ($1/2\ \sigma^2_A + 1/4\ \sigma_D = 2\sigma^2_{GCA} + \sigma^2_{SCA}$), where σ^2_A and σ^2_D signify additive and dominance variance.

We examined the lack of agreement between the GCA components for cross and OP progeny by comparing the contributions of the terms used in their computation. These terms for crosses are the GCA sum of squares, the SCA variance, and the error variance. For OP progeny, the SCA variance is missing. Generally these SCA variances in crosses were too small to be influential. For four of the five traits with low GCA components, SCA variances were significant: it is possible that for these traits they were important enough to reduce the GCA component below that for OP progeny. Error variances for the two classes of progeny were approximately equal after adjustment for the larger plot size (eight trees) for the OP progeny.

The larger GCA sums of squares for the OP progeny than for those from the crosses account for most of the difference in GCA components of variance. Thus, a limited number of males apparently resulted in OP families more like full-sibs than half-sibs. Hence, for these OP families, the contribution of the additive genetic variance to the variance was closer to $\sigma^2_{GCA} = 1/2\sigma^2_A$ than to the $\sigma^2_{GCA} = 1/4\ \sigma^2_A$ estimated in a controlled cross diallel experiment (Namkoong 1966).

To assess agreement in ranking parents for GCA values, the genetic correlations between the OP and the cross GCA's were computed, and they ranged from 0.93 to 0.29. Correlations were greater than 0.7 for 77 percent of the traits. The magnitude of the correlations was broadly proportional to the heritability of the trait shown in column 3. Traits with heritabilities higher than 0.21 generally had correlations of 0.85 or above. Traits with correlations below 0.60 were, with the exception of basal area (trait 16), either complex traits where measurement errors could accumulate or were discrete data.

It is not surprising that the GCA effects of 12 traits were significant for crosses (table 4, col. 5) but not for OP families, since these crosses have 12 times the genetic replication. However, the eight traits whose GCA effects were significant for OP's (col. 6) but not crosses require more consideration. That seven of these eight, all growth traits, had significant SCA effects (table 3) could mean that, *where heritabilities are low,* significant GCA effects for OP's may result from SCA rather than GCA effects. By contrast, SCA effects showed little influence on OP/cross ratios where heritabilities were high. This high frequency of significant SCA effects could also mean that single male influences on female family means inflated the OP family variances sufficiently that even the less precise estimates of those larger variances achieved significant levels. That is, the OP variances were larger because they estimated more genetic variances than they were expected to.

Thus, open pollination, when compared with controlled pollinations, generally estimated additive variances inaccurately but produced accurate GCA rankings—results similar to those obtained by Nilsson (1966).

Evaluation of Trait Inheritance

Table 5 presents the correlation coefficients reflecting GCA, SCA, and environmental relationships between each trait and each of the other traits evaluated in the study. Some of these data are referred to in the discussions which follow; all should become increasingly useful as breeding programs with longleaf pine progress into advanced generations.

Height. —There was little opportunity for studying variation in ability to grow out of the grass stage. First, exceptional hereditary growth capacity to grow rapidly out of the grass stage is a rare trait in longleaf pine, and unlikely to exist in a sample of only 13 parents (Snyder 1969). Secondly, planting and cultivation techniques in this experiment caused such unusually vigorous growth that average 5-year heights were 12 ft (3.7 m) and 7-year heights 20 ft (6.1 m) (table 6). Hence, families did not express the early height differences typical of most longleaf pine plantings.

Proportion of progeny trees 1 ft (0.3 m) or less in height at 3 years (trait 58) had a heritability of 0.01, indicating that in this experiment relative additive genetic variation was minimal. Trees in this class were excluded from subsequent analyses because their later growth was confounded with effects of brown-spot disease. More diagnostic of

Table 4.—*Correlations between General Combining Abilities (GCA) estimated from cross pollinations and those from open pollinations; with other statistics*

Trait number and name	Correlation coefficient	Cross heritability	GCA variance component ratio OP's/Crosses	GCA significant	
				Cross	OP
22 January bud length	.93	.62	1.6	X	X
44 Stomate density	.91	.56	1.5	X	X
45 Needle droop	.91	.29	1.1	X	X
2 March bud length	.90	.59	1.4	X	X
8 Branch angle at attachment	.90	.28	0.7	X	X
29 Branch/bole volume ratio	.90	.22	0.1	X	
30 Branch angle, (average)	.90	.43	1.8	X	X
31 Branch angle (attachment)	.88	.29	0.8	X	X
34 Needle length	.88	.34	0.4	X	X
38 Weight/needle	.88	.36	0.5	X	X
42 Stomate rows/cm of arc	.86	.47	1.6	X	X
48 Stem needle persistence	.86	.42	1.4	X	X
24 Bud diameter	.85	.27	1.5	X	X
43 Stomates/cm row	.85	.39	1.0	X	X
49 3-yr height, all trees	.84	.15	2.1	X	X
4 Bud scale width	.83	.12	1.1	X	
1 5-yr height	.82	.18	2.7	X	X
3 Bud scale length	.80	.20	0.3	X	
47 Branch needle persistence	.79	.16	0.8	X	
12 3-yr height, trees >1 ft	.78	.16	1.7	X	X
13 Height growth, 3rd to 5th yr	.77	.12	3.1		X
9 Needle number/ branch	.76	.15	0.4	X	
18 Length (bole section)	.76	.08	1.8	X	X
27 Branch/bole mid-diam' ratio	.75	.05	5.2		X
19 Basal area (bole section)	.74	.12	2.4	X	X
21 Volume (bole section)	.74	.08	3.2		X
35 Needle perimeter	.74	.26	0.4	X	
10 Needle weight/branch	.72	.18	0.1	X	
28 Number of 5th yr branches	.72	.21	0.7	X	X
46 Branch length	.72	.19	1.2	X	X
15 7-year height	.71	.12	3.4	X	X
25 Bud scale length, adj.	.71	.14	1.4	X	X
26 Branch length/tree height ratio	.69	.17	0.5	X	
14 Height growth, 5th to 7th yr	.55	.05	3.5		X
17 7-yr tree volume	.54	.07	4.1		X
16 7-yr basal area	.52	.08	3.4		X
20 Bole taper factor	.51	.06	2.7	X	
59 Trees with fusiform rust	.48	.12	0.6	X	
50 7-yr survival,	.47	.03	10.1	X	X
51 Plot volume	.47	.03	4.5		X

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Table 4.—*Correlations between General Combining Abilities (GCA) estimated from cross pollinations and those from open pollinations; with other statistics*

Trait number and name	Correlation coefficient	Cross heritability	GCA variance component ratio OP's/Crosses	GCA significant	
				Cross	OP
52 Plot volume, bole section	.36	.03	6.3		X
23 Bud length growth	.35	.14	0.3	X	
33 Knot area/bole diam^2 ratio	.29	.07	1.2	X	

[1]Only traits with significant GCA's are shown

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Table 6.—General Combining Ability (GCA) statistis for constituents of height and height growth, with related statistics. In the upper section of the table, on and above the diagonal are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations.

Component $\times 10^5$

Item	58 Trees >1 ft at 3 yrs	49 3-yr height all trees	12 3-yr height trees >1 ft	1 5-yr height	15 7-yr height	13 Height growth 3rd to 5th yr	14 Height growth 5th to 7th yr
Trait							
58 Trees >1 ft at 3 yrs	256892 ±187874	38763 ±17398	35252 ±14568	52229 ±22844	1050 ±557	16904 ±8267	−8423 ±1565
49 3-yr height, all trees	0.89	7346 ±3060	7022 ±2906	11284 ±4699	252 ±108	4267 ±1793	483 ±284
12 3-yr height, trees >1 ft	.85 / —	1.00 / 0.93	6752 ±2819	10954 ±4606	254 ±108	4210 ±1788	860 ±408
1 5-yr height	.72 / —	.92 / .81	.94 / .88	20219 ±8990	461 ±215	9297 ±4397	1307 ±887
15 7-yr height	.63 / —	.88 / .72	.92 / .78	.96 / .91	11 ±5	207 ±107	69 ±42
13 Height growth, 3rd to 5th yr	.47	.70 / .48	.72 / .53	.91 / .86	.86 / .81	5110 ±2622	454 ±490
14 Height growth, 5th to 7th yr	−.37 / —	.13 / .24	.24 / .24	.21 / .29	.47 / .64	0.14 / .28	1930 ±1008

Unit

Statistic	58 Arc sine $\sqrt{pct}$	49 Ft	12 Ft	1 Ft	15 Log inch	13 Ft	14 Ft
Mean	80.98	3.01	3.17	11.98	2.39[1]	8.80	8.66
CV phenotypic [2]	19	29	26	11	2	9	8
σ^2 phenotypic	232.19837	1.99720	1.67543	4.57452	.003658	1.67433	1.5366
σ^2 Plot (or error)	227.16757	0.25831	0.19423	0.61120	0.00040	0.14930	0.03042
σ^2 W thin/k²	—	.49812	.48922	1.26837	.00105	.49171	.51180
h² Individual	0.01	.15	.16	.18	.12	.12	.05
h² Replicated	.04	.36	.38	.34	.25	.26	.19

[1]Equivalent to 20.5 feet

[2]Coefficient of variation = [(error M.S.) ½/mean] x 100

[3]k = harmonic mean number of trees per plot

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early height growth ability under conditions of the experiment is 3-year height of trees >1 ft (0.3 m) (trait 12) which had a mean of 3.2 ft (1.0 m), a heritability of 0.16, and a significant GCA variance component.

At 5 years, when mean heights were 12 ft (3.7 m) the GCA component of height was significant, and the heritability was 0.18. At 7 years, when mean height was 20 ft (6.1 m), the GCA component was significant but the heritability was 0.12. Growth from the fifth to seventh year (trait 14, $h^2 = 0.05$), genetically uncorrelated with previous height, was associated with this decrease in heritability.

General Combining Ability correlations of later measurements with 3- and 5-year height were high (r from 0.72 to 0.96). An exception was the 5- to 7-year growth increment which had a correlation of only 0.24 with 3-year height and of 0.21 with 5-year height. Correlations of 0.92 and 0.96, respectively, between 3-year and 5-year heights and 7-year height show that early height growth affects later height through age 7. The reduced correlations with 5- to 7-year increment, however, suggest weakening of such correlations in the future.

Tree and Plot Volume. — Constituent traits combined to evaluate plot volume (trait 51) are survival (trait 50), tree height (trait 15), and basal area (trait 16). Table 7 presents GCA and other statistics for this group of traits. The GCA components of survival and height are significant. Survival is the more important, contributing 58 percent to the variance of plot volume; if it is deleted from the selection index representing volume, gain is reduced by 40 percent.

Individual tree volume (trait 17) is computed from height and basal area. In these progeny, basal area contributed more than height to the mean, variance, and selection index for volume. Differences in contribution to selection index were small, however, the loss in gain being 3 percent if height is excluded and 7 percent if basal area is excluded. These low values are consistent with the 0.81 phenotypic correlation between the two characters but are unexpected in view of their rather low 0.30 genotypic correlation. Thus, the impact of a trait on a selection index is unpredictable from the size of a single statistic for it.

Percentage gains at 7 years, computed as outlined on pg. 8, p. 2 and with a proportion selected of 1 in 100 (i = 2.665) were:

15	Height	9.3
16	Basal area	13.9
17	Individual tree volume	17.0
50	Survival	5.8
51	Plot volume	6.8

These gains, although worthwhile, are not nearly so large as those generally encountered with longleaf pine (Snyder 1969). Larger gains depend on detecting rare individual parents not represented in the small sample of this experiment. Perhaps better survival and plot volume gains would have been predicted had experimental conditions resulted in less uniformly high survival (88 percent) and thus a better expression of genetic survival capacity.

The correlation between parental phenotypes and GCA values derived from their progeny was 0.43 for height and -0.03 for basal area (table 2). The relatively high parent-progeny relation for height growth suggests considerable gain from parents selected for height growth; no gain should occur when selection is based on parental diameters. Most published results also assert higher gain from heights than from diameters, but greater gain from diameter selection in two slash pine progeny tests[1] cautions against generalizing.

In addition to their relations to constituent traits, tree and plot volume were found to be genetically correlated with a number of other traits. Tree volume (trait 17) was related to both foliage weight (trait 39) and branch length/tree height ratio (trait 26) with r values of 0.84. These two traits are also highly correlated with each other (r = 1.00).

Tree height at 3 years (trait 12) was better correlated with tree volume (trait 17), GCA r = 0.82, than was 7-year height (trait 15), r = 0.66 (table 6). Although the estimates are made with large error, 3-year height is apparently as good an indication of 7-year volume as is 7-year height.

Tree survival, a major contributor to plot volume, we found to be strongly correlated with bud length. Families with long buds in January or in March (traits 22, 2) tend to be poor survivors (trait 50), GCA r = -0.75, -0.71. Perhaps such early starting trees can not minimize drought effects later in the growing season. Selection for shorter buds could be a useful approach to increased survival and thus to higher volume per acre.

[1]Results on file, Forestry Sciences Laboratory, Gulfport, Miss.

Table 7.—*General Combining Ability statistics for constituents of volume, with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

Item	Trait 50 7-yr survival	15 7-yr height	16 7-yr basal area	51=50+15+16 Plot volume	17=15+16 7-yr tree volume
			Log Component x 10^0		
Trait					
50 7-yr survival	820 ±369	61 ±30	−75 ±20	811 ±385	−20 ±18
15 7-yr height	.20 .10	113 ±56	60 ±50	234 ±136	174 ±106
16 7-yr basal area	−.14 .07	.30 .81	362 ±192	346 ±224	426 ±243
51 Plot volume	.76 .73	.59 .67	.49 .70	1394 ±747	578 ±360
17 7-yr tree volume	−.03 .08	.66 .90	.91 .98	.63 .72	603 ±350
Contribution to Plot volume			Percent		
Mean	23	29	48	—	—
Variance (range)	58 ±1	17 ±9	25 ±1	—	—
Selection index	40	1	10	—	—
Contribution to individual volume			Percent		
Mean	—	38	62	—	—
Variance (range)	—	29 ±10	71 ±10	—	—
Selection index	—	3	7	—	—
Statistics			Units		
	Log pct+2	Log inch	Log inch²+3	Log inch³+5	Log inch³+3
Mean	1.8597	2.3897	3.8871	8.1343	6.2772
CV phenotypic	8	2	2	2	2
σ^2 phenotypic	0.023849	0.003658	0.017520	0.042160	0.033519
σ^2 plot (or σ^2 error)	.022968	.000404	.001984	.038294	.004067
σ^2 within/k^1	—	.001055	.005113	—	.009622
h^2 individual or plot	.03	.12	.08	.03	.07
h^2 replicated	.12	.25	.18	.10	.16

[1] k = harmonic mean number of trees per plot

Measurements confined to the 5th year section of the bole were expected to reflect mature growth patterns better than those taken from the total tree which was predominantly of younger material. However, negative GCA correlations between height and basal area of the bole section, and the existence of large SCA effects (table 5, see insert) suggest that the data are unrepresentative of long-term growth. Because tree size varied greatly from replication to replication, it is possible that strong genotypic × replication interactions affected relations between these traits.

Taper (trait 20), another constituent of bole volume, had GCA correlations with basal area (trait 16) and volume (trait 17) of 0.83 and 0.82. Because of this close positive association, it would not be practical or necessary to breed separately for this character in trees similar to those in this study.

Foliage. —Foliage surface (trait 37) and foliage weight (trait 39) are related traits; their GCA correlation coefficient was 0.97. Foliage weight is more important genetically because of its stronger relation to volume, with which it had a GCA correlation of 0.84 (table 5, see insert). According to the selection index for foliage surface, branch number (trait 28) contributed more genetically to foliage surface than did needle length (trait

Table 8.—*General Combining Ability statistics for constituents of foliage surface, with related statistics. In the upper section of the table, on and above the diagonal are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

Item	28 No. 5th-yr branches	34 Needle length	35 Needle perimeter	36 Needles/branch	37=28+34+35+36 Foliage surface
	· Log component x 10° ·				
Trait					
28 No. 5th yr branches	1435 ±619	−214 ±84	−139 ±52	151 ±69	1146 ±577
34 Needle length	−0.55 −.09	104 ±45	68 ±28	12 ±9	−104 ±37
35 Needle perimeter	−.47 −.08	0.85 .60	61 ±25	−32 ±14	−106 ±37
36 Needles/branch	.21 .23	.06 .10	−0.21 .04	370 ±199	617 ±292
37 Foliage surface	.78 .63	−.26 .09	−.35 .10	0.82 .48	1519 ±932
Contribution to foliage surface	-- Percent --				
Mean	11	22	23	44	—
Variance (range)	74 ±12	−2 ±8	−2 ±6	30 ±8	—
Selection index	42	0	2	6	—
Statistics	-- Unit --				
	Log no.	Log cm	Log cm + 2	Log no.	Log cm² + 2
Mean	0.7413	1.5422	1.5802	2.9831	6.8472
CV phenotypic	14	1	1	2	4
σ^2 phenotypic	.027555	0.001207	0.000952	0.013475	0.051862
σ^2 plot	.003143	.000126	.000033	.000545	.070581
σ^2 within/k[1]	.008085	.000329	.000297	.004354	−.007805
h^2 individual	.21	.34	.26	.11	.12
h^2 replicated	.38	.50	.55	.32	.08

[1]k = harmonic mean number of trees per plot

34), needle perimeter (trait 35), or needles per branch (trait 36) (table 8). Needle length (trait 34) could be omitted without loss of genetic information. Similarly, weight per needle (trait 38) contributed little to foliage green weight (table 9). Both foliage surface (trait 37) and foliage weight (trait 39) were genetically correlated with branch length (trait 46), r = 0.83, 0.85.

Foliage surface and foliage weight allometrically adjusted to bole volume (traits 40, 41, table 10), had nonsignificant GCA components and low heritabilities. This result could mean a near perfect fit of adjusted foliage values and bole section volume (trait 21), or the fit may be so poor that

Table 9.—*General Combining Ability statistics for constituents of foliage weight, with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations; lower values are phenotypic correlations.*

		Trait			
	Item	28 No. 5th-yr branches	36 Needles/branch	38 Green wt/needle	39=28÷36+38 Foliage wt
		------Log Component x 10^5------			
	Trait				
28	No. 5th-yr branches	144 ± 62	15 ± 7	-29 ± 11	112 ± 55
36	Needles/branch	0.21 .23	37 ± 20	-7 ± 3	52 ± 23
38	Green wt/needle	$-$.38 .02	-0.17 .09	41 ± 17	-7 ± 2
39	Foliage wt	.79 .64	.72 .49	-0.09 .19	141 ± 81
Contribution to Foliage wt		------Percent------			
Mean		18	72	10	—
Variance (range)		72 ± 8	25 ± 4	3 ± 20	—
Selection index		56	2	0	—
Statistics		------ Units ------			
		Log no.	Log no.	Log g + 1	Log g + 1
Mean		0.7413	2.9831	0.4223	4.1458
CV phenotypic		14	2	10	5
σ^2 phenotypic		.02756	0.01348	.00457	0.04994
σ^2 plot		.00314	.00054	.00074	.05541
σ^2 within/k^1		.00808	.00435	.00118	$-$.00264
h^2 individual		0.21	0.11	0.36	0.11
h^2 replicated		.38	.33	.53	.09

^{1}k = harmonic mean number of trees per plot

Table 10.—*General Combining Ability statistics for two measures of crown efficiency, with related statistics. In the upper section of the table, on and above the diagonal, are GCA variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

	Trait	
Item	40 Adjusted foliage surface[1]	41 Adjusted foliage wt[1]
	Log component x 10^6	
Trait		
40 Adjusted foliage surface	774 $\pm$ 459	801 $\pm$ 426
41 Adjusted foliage wt	0.95 .80	914 $\pm$ 466
Statistics	------------------------------Units------------------------------	
	Log cm^2	Log g
Mean	.001	0.003
CV phenotypic	—	—
σ^2 phenotypic	.038696	.036610
σ^2 plot	.017150	.004398
σ^2 within/k^2	.007019	.010892
h^2 individual	.08	.10
h^2 replicated	.11	.24

[1] $\hat{Y}(40) = Y(37) - 3.4386 - 0.6208\ Y(21)$

$\hat{Y}(41) = Y(39) - 0.4866 - 0.6666\ Y(21)$

where 21, 37, 39 take the values of these traits. See text for details of this allometric adjustment.

[2] k = harmonic mean number of trees per plot

large fitting errors in genetic effects cause non-significance. Since the genetic correlations between foliage values and bole volume are only 0.65 and 0.55 (table 5, see insert), we favor the latter hypothesis.

Parent-progeny correlations for needle length (trait 34), needle perimeter (trait 35), needle weight (trait 38), and needles per branch (trait 9) were: 0.61, 0.68, 0.70, and 0.34 (table 2). These results indicate a potential for gains from parental selection for these needle characteristics and strongly suggest that variations in these characters measured at age 7 will persist to maturity.

Branches.—Constituents of branch/bole volume ratio (trait 29) are branch length/tree height (trait 26), branch/bole mid-diameter[2] ratio (trait 27), and branch number (trait 28) (table 11).

Because of the low contribution of branch/bole mid-diameter[2] ratio, this trait could be eliminated as a constituent. On the other hand, because the composite trait branch/bole volume ratio (trait 29) has a larger heritability (h^2) than any of its constituents, both it and its other two constituents, branch length/tree height ratio and branch number, should be useful in selection practices.

An important reason for examining branch traits is to determine how selection for short, small diameter branches would affect bole volume. Since the GCA correlation of bole volume (trait 17) with branch length/tree height was 0.84, volume growth should decrease if parents are chosen for short branches. Selection for a large branch length/tree height ratio is indicated. Selection of parent trees for crown efficiency, i.e., fast growth with

Table 11.—*General Combining Ability statistics for constituents of branch/bole volume ratio and related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations; lower values are phenotypic correlations*

Item	26 Branch length/tree ht ratio	27 Branch/bole mid-diam² ratio	28 Number 5th yr branches	29=26+27+28 Branch/bole volume ratio
			Trait	
			Log component x 10⁵	
Trait				
26 Branch length/ tree ht ratio	73 ± 31	−20 ± 8	76 ± 29	132 ± 54
27 Branch/ bole mid-diam² ratio	−0.48 −.25	23 ± 12	−43 ± 19	−40 ± 15
28 Number 5th-yr branches	.75 .20	−0.76 −.36	143 ± 62	173 ± 72
29 Branch/ bole volume ratio	.95 .60	−.52 .15	0.89 .67	264 ± 112
17 7-yr tree volume	.84 .54	−.44 −.42	.50 .50	0.72 .46
Contribution to branch/bole volume ratio		Percent		
Mean	60	−8	49	—
Variance (range)	49 ± 21	−15 ± 24	66 ± 12	—
Selection index	20	2	27	—
Statistic	Units			
	Log ratio +1	Log ratio + 1	Log ratio	Log ratio + 2
Mean	.9125	−.1290	.7413	1.5259
CV phenotypic	9	67	14	10
σ^2 phenotypic	.01714	.01872	.02756	.04896
σ^2 plot	.00203	.00147	.00314	.00749
σ^2 within/k[1]	.00520	.00605	.00808	.01357
h² individual	.17	.05	.21	.22
h² replicated	.40	.14	.38	.40

[1]k = harmonic mean number of trees per plot

small crowns, thus appears difficult. This trait warrants more study as crowns close in these test plantings.

Knot area/bole diameter^2 ratio (trait 33) is an index of economic value whose constituents are branch angle (trait 31) and branch/bole diameter^2 ratio (trait 32) (table 13). Despite its low contribution to the mean or variance, branch angle contributed 29 percent to the selection index compared to 11 percent for the branch/bole diameter^2 ratio.

The overall branch angle (trait 30) should be diagnostic in identifying mixtures of ramets as to clone because of its relatively large heritability of 0.43 (table 13). The angle of attachment (trait 8) had less additive variance, $h^2 = 0.28$. The GCA correlations of branch length and measures of angles in degrees were negative, contrary to results sometimes obtained with older trees. Thus, selection for trees combining short branches with horizontal branch angles may be feasible. It may not be desirable, however, because the correlations of branch length ratio with height growth and stem volume are positive; short-branched trees would tend to grow more slowly in height and volume.

Of the three branch characters tested for parent-progeny relations (table 2), branch/bole mid-diameter^2 ratio (trait 27) had a correlation of 0.62, branch angle (trait 8) 0.59, and branch length/tree height ratio (trait 26) only 0.16. The low parent-progeny correlation for branch length indicates that parental selection for juvenile branch length has little value for breeding. This cor-

Table 12.—General Combining Ability statistics for branch length and angle, with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations

Item	Trait		
	46 Branch length	8 Branch angle at attachment	30 Branch angle, average
	----------------------------Component x 10^4----------------------------		
Trait			
46 Branch length	26 ± 11	-477 ± 203	-554 ± 220
8 Branch angle at attachment	-0.54 $-.08$	30247 ± 12461	41021 ± 16208
30 Branch angle, average	$-.42$ $-.10$	0.92 $.65$	65570 ± 26266
Statistic	------------------------------- Units -------------------------------		
	$\sqrt{\text{Feet}}$	Degree	Degree
Mean	1.907	67.33	62.70
CV phenotypic	8	6	8
σ^2 phenotypic	.0541	43.2514	61.5767
σ^2 plot	.0075	3.6772	4.1584
σ^2 within/k[1]	.0157	13.0738	18.1488
h^2 individual	.19	.28	0.43
h^2 replicated	.37	.51	.63

[1]k = harmonic mean number of trees per plot

Table 13.—*General Combining Ability statistics for constituents of knot area/bole diam² ratio, with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

Item	Trait 31 Branch angle	Trait 32 Branch/bole diam² ratio	Trait 33=31+32 Knot area/bole diam² ratio
	----------Log component x 10^6 ----------		
Trait			
31 Branch angle (attachment)	30 $\pm$ 12	16 $\pm$ 9	46 $\pm$ 21
32 Branch/bole diam² ratio	0.19 .26	221 $\pm$ 111	240 $\pm$ 121
33 Knot area/bole diam² ratio	.49 .41	0.95 .98	288 $\pm$ 143
Contribution to area	----------Percent----------		
Mean	−4	104	—
Variance (range)	16 $\pm$ 6	84 $\pm$ 6	—
Selection index	29	11	—
Statistic	---------- Units ----------		
	Log cosec. angle	Log ratio	Log ratio
Mean	0.0387	−1.0161	−0.9769
CV phenotypic	32.	8	9
σ^2 phenotypic	.000418	0.015725	.017195
σ^2 plot	.000022	.001253	.001631
σ^2 within/k^1	.000132	.005124	.005400
h^2 individual	.29	.06	.07
h^2 replicated	.59	.18	.20

[1]k = harmonic mean number trees per plot

relation should not be applied to other situations, however, without further study. Barber (1964) found much higher parent-progeny correlations for branch length in slash pine. His findings could reflect a species difference or could result from a more uniform parental growing environment. Our study parents, grown in a semi-open stand and subjected to variable competition, may have acquired excessive phenotypic variation in branch length.

Trees with fusiform rust, trees forking.—Our data did not support the tradition that fusiform rust is innocuous to longleaf pine. We found wide variation in susceptibility (trait 59) in our population sample; six families were quite resistant, six moderately resistant, and one rather susceptible. Twenty-five percent of the progeny derived from crossing the two most susceptible parents were infected whereas the average infection was 6.5 percent. The susceptible family was conspic-

uous because longleaf is considered a relatively resistant species. Resistance being generally common, however, and susceptibility rare, a simple roguing of parents producing susceptible progeny should be adequate to exclude fusiform rust susceptibility from genetically improved longleaf pine.

Although the GCA variance component for infection was significant, the heritability was only 0.12 (table 14). Low average infection, the attribute nature of the trait, and the small four-tree plots combined to give a coefficient of variation of 51 percent and an unimpressive heritability.

The genetic correlations with other traits (table 5, see insert) suggest a possible source of susceptible genes (fig. 2). Five traits—basal area, bole section basal area, bole section taper factor, branch length/tree height ratio, and foliage surface (trait numbers 16, 19, 20, 26 and 37, respectively)—all of them measures of growth—were highly and positively related to rust occurrence. As values for these traits increase, rust susceptibility also increases. Two other highly related traits, branch/bole mid-diameter^2 ratio (trait 27)

and bud diameter (trait 24) varied inversely with susceptibility. Because loblolly pine has relatively smaller branches and buds than longleaf, traits 27 and 24 have been used in other studies as morphological indices of introgression with loblolly pine. The data thus present some evidence for a complex of growth-morphologic-rust-resistance traits associated with introgression. We hypothesize that breeding longleaf for increased growth rate via introgression may also increase rust susceptibility.

The other discrete trait, forking, occurred in 20 percent of the study progeny. Such forking, often largely due to insect attack on terminal buds, is not unusual in young, fast-growing longleaf plantations. Forking in this study was weakly but significantly heritable (table 14). The heritability, $h^2 = 0.06$, calculated for four-tree plots, may be an underestimate. When data are calculated on an eight-tree plot basis by pooling reciprocals, heritability value is increased. The four-tree plots, although adequate for other traits, appear to be too small to determine heritability of this

Table 14.—*General Combining Ability statistics for incidence of forking and fusiform rust, with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

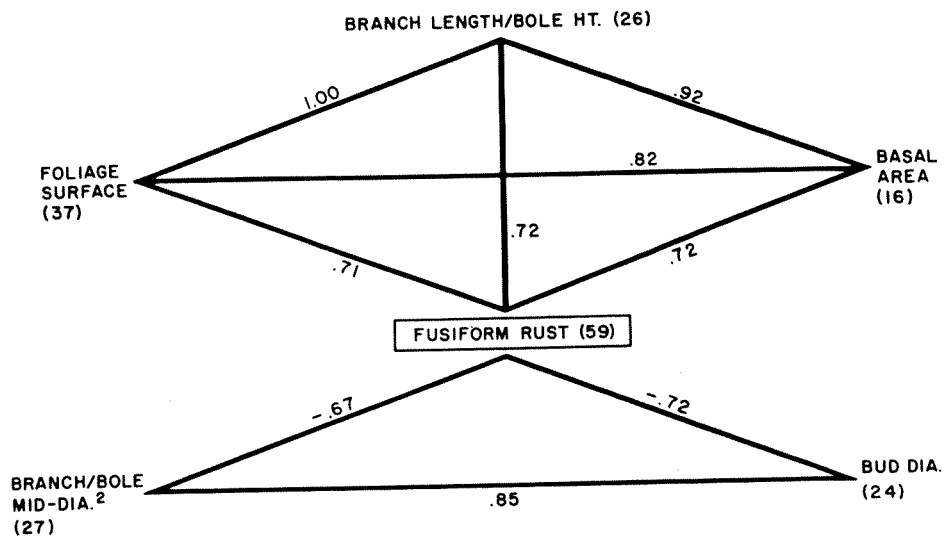|	Trait	
Item	57 Trees forking	59 Trees with fusiform rust
Trait	------------------ Component x 10^2 ------------------	
57 Trees forking	1382 ± 562	− 233 ± 81
59 Trees with fusiform rust	−0.14 .02	1718 ± 710
Statistic	-------------------- Arc sine $\sqrt{pct}$ --------------------	
Mean	32.8 (20 percent)	21.6 (6 percent)
CV phenotypic	45	51
σ^2 phenotypic	233.4	146.9
σ^2 error	220.1	122.7
h^2 plot	.06	0.12
h^2 replicated	.20	.31

Figure 2.—*Some genetic correlation relationships with fusiform rust incidence.*

trait adequately. Heritabilities are too low to require strenuous roguing of individuals or families, but badly forked trees should, of course, be eliminated by thinning in young plantations and seed orchards.

Needles.—The relations of dorsal stomate density (trait 44) to its constitutents, number of rows/cm of arc (trait 42) and number of stomates/cm of row (trait 43), are shown in table 15.

Although expensive to measure, the stomate traits were among the most heritable ($h^2 = 0.39$ to 0.56) of those studied. The selection index for stomate density reveals that number of rows is more important genetically than the number of stomates within rows, but the higher h^2 for the composite trait suggests its use in research and breeding.

The number of stomates per cm^2 of dorsal leaf surface was inversely correlated with adjusted foliage surface area (trait 40), genetic r = —0.97. Thus, there is a trend toward a constant total number of stomates per tree. This regulation was achieved in part through branch number (trait 28), which was related to stomate density with a genetic r = —0.79. Also, the larger the branch/bole volume ratio (trait 29), the fewer the stomates (r = —0.72). The tendency toward constancy of stomate number should be investigated for its biological meanings and possible usefulness in breeding.

Stomate density is the only trait showing a significant reciprocal effect. Since this was only 11 percent of the total genetic variance, reciprocal effects can be ignored for longleaf pine under our conditions.

The seven other needle characters (table 16) all had significant GCA variance components, and their heritabilities were among the highest of the traits studied.

Needle droop (trait 45), an inverse measure of stiffness, had been of interest chiefly for identification purposes but is a member of a complex of traits that may be involved indirectly in volume growth (trait 17)—the genetic correlation of droop with volume was —0.55 and with foliage surface —0.73. Needle droop also varied inversely with the number of needles per branch (trait 9) and directly with needle weight (trait 38) and needle length (trait 34).

The genetic correlations indicate that progeny with a considerable proportion of the branch covered with needles (trait 47) inherently tend to have long, heavy needles (traits 34, 38), r =0.70, 0.74, and high needle weight per branch (trait 10), r = 0.62. The correlation of needle persistence with heights and volumes, however, was small and negative.

A striking trait was the tendency of some families to retain their juvenile stem needles (trait 48) even though trees were fully branched and 10 to 20 ft (3.0 to 6.1 m) tall. This retention trait was highly heritable, $h^2 = 0.42$, and genetically correlated with many, heavy, and long branch

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Table 15.—*General Combinging Ability statistis for constituents of total stomates/cm², with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

Item	Trait		
	42 Stomate rows/cm of arc	43 Stomates/cm of row	44 = 42 + 43 stomates/cm²
Trait	----------------------------Component x 10⁶----------------------------		
42 Stomate rows/cm of arc	166 ± 64	36 ± 13	202 ± 78
43 Stomates/cm of row	0.29 .10	91 ± 36	127 ± 49
44 Stomates/cm²	.86 .80	0.73 .68	328 ± 127
Contribution to total	---------------------------- Percent ----------------------------		
Mean	46	54	—
Variance (range)	61 ± 11	39 ± 11	—
Selection index	34	16	—
Statistic	---------------------------- Log no. ----------------------------		
Mean	1.6791	2.0103	3.6895
CV phenotypic	1	1	1
σ^2 phenotypic	.001426	.000942	0.002356
σ^2 plot	−0.000013	.000018	.000029
σ^2 within/k[1]	.000442	.000287	.000705
h² individual	.47	.39	.56
h² replicated	.75	.65	.76

[1]k = harmonic mean number trees per plot

needles (traits 9, 10, 38, 34), but was weakly or negatively correlated with volume.

Traits 10, 34, 35, and 38—needle weight per branch, needle length, needle perimeter (not shown in table), and weight per needle—were related genetically to branch diameters (trait 27), r = 0.77, 0.97, 0.90 and 0.74, respectively, and to knot area (trait 33), r = 0.71, 0.77, 0.71, 0.55, respectively (table 5, see insert).

Parent-progeny correlations were high for six of the seven needle traits tested, that for stomates/cm of row being highest, 0.80 (table 2).

The other correlations were 0.53 or higher, except for needles/branch (trait 9), which was 0.34.

Buds. Although all bud scale dimension traits had significant additive variance components, the heritabilities, 0.12 to 0.20 are relatively low (table 17). When allometrically adjusted to eliminate growth effects (trait 25), bud scale length showed a heritability of 0.14 instead of the 0.20 calculated from unadjusted measurements. Potentially interesting to tree breeders is the high negative correlation (r = −0.72) between adjusted bud scale length (trait 25) and 3-year height (trait 49). Since

Table 16.— *General Combining Ability statistics for seven needle traits, with related statistics. In the upper section of the table, on and above the diagonal, are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

Item		45 Needle droop	47 Branch needle persistence	48 Stem needle persistence	Trait 9 Needle number/branch	10 Needle weight/branch	38 Weight/needle	34 Needle length
		Component x 10^2	Component x 10^2	Component x 10^2	Component x 10^1	Component x 10^1	Component x 10^6	Component x 10^5
Trait								
45	Needle droop	385 ± 161	88 ± 44	102 ± 39	−39 ± 13	1 ± 1	2007 ± 773	1109 ± 484
47	Branch needle persistence	0.37 / .16	148 ± 77	220 ± 90	2 ± 3	12 ± 5	1839 ± 671	865 ± 357
48	Stem needle persistence	.20 / .10	0.70 / .54	661 ± 264	66 ± 24	29 ± 11	2001 ± 751	1452 ± 539
9	Needle number/branch	−.45 / .00	.05 / −.12	0.58 / −.13	1988 ± 882	422 ± 193	−17554 ± 6806	2511 ± 1479
10	Needle weight/branch	.05 / .12	.62 / −.05	.74 / −.10	0.61 / .86	242 ± 105	20994 ± 8595	13203 ± 5289
38	Weight/needle	.50 / .24	.74 / .07	.38 / .01	−.19 / .08	0.66 / .56	41 ± 17	20 ± 8
34	Needle length	.55 / .49	.70 / .15	.55 / .10	.06 / .10	.83 / .35	0.96 / .54	10 ± 4

Statistics	Degrees	Arc sine √pct	Arc sine √pct	Units No.	G	Log g + 1	Log cm
Mean	28.14	43.96	38.52	1002	268.7	0.4223	1.5422
CV phenotypic	15	9	12	14	17	10	1
σ² Phenotypic	52.83	35.89	62.61	53266	5308	0.00457	0.001207
σ² Plot	4.27	4.88	1.10	3099	411	.00074	.000126
σ² within/k¹	15.43	10.48	18.72	16909	1623	.00118	.000329
h² individual	0.29	0.16	0.42	0.15	0.18	.36	.34
h² replicated	.53	.33	.65	.43	.43	.53	.50

¹k = harmonic mean number trees per plot

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bud scale dimensions are expensive to measure, however, this cost may not be justified for studies of longleaf pine.

Contrary to expectation, bud scale width (trait 4) was found to be genetically correlated with bud length (trait 22), r = 0.77, and bud scale length (trait 25) was correlated with bud diameter (trait 24), r = 0.76, while correlations between scale and bud widths, and between scale and bud lengths were low, r = 0.14 and 0.31, respectively.

Traits 22 and 2, January and March bud lengths, were the most heritable in the study, in part, perhaps, because they were measured before spring growth had introduced differential phenological responses. Lower heritabilities of other leaf and bud traits may reflect their measurement during the growing season, when different growth stages due to environment would be encountered.

Bud length (trait 2) is related to a different set of traits than bud diameter (trait 24). Bud length is related to bud scale width (trait 4), r = 0.76; to foliage surface allometrically adjusted (trait 40), r = 0.79; and to survival (trait 50), r = −0.71. Bud diameter is related to bud scale length (trait 25), r = 0.76; to needle perimeter (trait 35), r = 0.79; to branch diameter (trait 27), r = 0.85; and to fusiform rust susceptibility (trait 59), r = −0.72. It is weakly or negatively genetically correlated, however, with stem diameter and volume.

The parent-progeny correlation for bud scale

Table 17.—*General Combining Ability statistics for bud scale dimensions with related statistics. In the upper section of the table, on and above the diagonal are variance and covariance components with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

	Trait		
Item	4 Bud scale width	3 Bud scale length	25 Bud scale length, adjusted[1]
Trait	--------------------------------Component x 10^5--------------------------------		
4 Bud scale width	709 ± 301	4269 ± 1728	40 ± 15
3 Bud scale length	0.78 .64	41739 ± 18318	667 ± 303
25 Bud scale length, adjusted	.41 .08	0.89 .91	401 ± 149
Statistic	--------------------------------Units--------------------------------		
	mm	mm	Log mm
Mean	3.30	16.4	0.001
CV phenotypic	10	11	—
σ^2 phenotypic	.23531	8.26029	.00378
σ^2 plot	.04875	.87101	.00012
σ^2within/k^2	.06355	2.46318	.00123
h^2 individual	.12	.20	.14
h^2 replicated	.29	.49	.45

[1]$\hat{Y}$ (25) = Log (3) − 0.8044 − 0.7840 Log (4) where 3 and 4 take values of the respective characters. See text for details of this allometric adjustment

[2]k = harmonic mean number trees per plot

length (trait 3) was 0.74, for bud scale width (trait 4) 0.61, for bud length (trait 22) 0.56, for bud length growth (trait 23) 0.32, and for bud diameter (trait 24) 0.86 (table 2).

Discussion

The generally successful controlled pollinations and the high survival of replicated progeny outplantings in this experiment afforded precise data for evaluations of the parents sampled. The analytical procedures, involving natural grouping of traits, were useful in analyzing trait relationships although somewhat deeper insights may be possible when techniques of multivariate analysis become available for such a study. Unavoidable limitation of the study to 13 individual parents and to two outplantings calls attention to the need for additional experiments. Meanwhile, the results do afford findings that scientists and tree breeders should find useful in the formulation of breeding strategies for longleaf pine.

Correlations between traits varied widely. As expected, correlations were generally high between composite traits and their constituents, and be-

Table 18.—*General Combining Ability statistics for bud dimensions with related statistics. In the upper part of the table, on and above the diagonal, are variance and covariance components, with standard errors; below the diagonal, upper values are GCA correlations, lower values are phenotypic correlations*

Item	Trait			
	24 Bud diameter	2 March bud length	22 Jan. bud length	23 Jan.-March growth in bud length
	---------------------------------- Component x 10^4 ----------------------------------			
Trait				
24 Bud diameter	377 ± 153	105 ± 51	80 ± 39	31 ± 15
2 March bud length	0.12 .22	1856 ± 729	1464 ± 569	447 ± 180
22 Jan. bud length	.12 .25	1.00 0.87	1156 ± 453	346 ± 132
23 Jan.-March growth in bud length	.15 .06	.95 .66	0.94 .25	118 ± 54
Statistics	---------------------------------- Units ----------------------------------			
	mm	cm	cm	cm
Mean	9.97	5.104	4.301	0.815
CV phenotypic	7	13	12	46
σ^2 phenotypic	2.2200	1.2595	.7477	.3371
σ^2 plot	−0.3355(0)[1]	.1058	.0667	.0446
σ^2 within/k^2	.8920(0.1843)	.3354	.1933	.0988
h^2 individual	.07(0.27)	.59	.62	.14
h^2 replicated	1.00(.83)	.71	.69	.36

[1]Results if this component is considered as zero and mean squares are pooled

[2]k = harmonic mean number trees per plot

tween traits based on related morphological features. In some cases, too, high correlations between apparently unrelated traits were revealed that afford opportunities to strengthen breeding practices by indirect selection. Thus, dormant season bud length had a correlation of -0.8 with tree survival. More obvious are the high correlations between tree volume and foliage weight (0.84) and between tree volume and the ratio of branch length to bole height (0.84). Such relationships offer approaches by which tree breeding for volume production might be supplemented by selection for correlated traits as well as the more obvious constituents.

The study revealed significant GCA effects for 35 of the 51 traits and SCA effects for 25 of them; the latter were of small size and at present are mainly of academic interest. Heritabilities varied from 0.01 to 0.62. Traits with higher heritabilities were those such as bud dimensions, which change seasonally but were measured in the dormant season. They should be excellent markers for identification purposes.

Relationships between composite traits and the simpler ones from which they are formed are useful to geneticists and tree breeders. If linear functions of constituent traits are adequate to quantify the composites, and the heritability of the composite is no higher than those for the constituents, then breeding for the constituents alone is effective; otherwise, breeding for both the composite and constituents is called for. The latter procedure is also advised as a safeguard against obtaining an undesirable correlated response in one trait while selecting for another. Williams (1964) pointed out another advantage of including constituents—one or more may show less $G \times E$ interactions than the composite.

Of seven composite traits analyzed, tree volume, plot volume, foliage surface, foliage weight, knot area, branch volume, and total stomates, the last two had higher heritabilities than their constituent characters. For these two traits, genetic effects may be acting on the composite trait more directly than on the constituents. Both composite and constituent traits should be included in selection indices of such characters.

These analyses also suggest possibilities for elimination of specific traits from future studies. Thus, needle dimensions and weight contributed little to genetic variation in foliage quantities; if some of these unessential parameters can be dispensed with, future research costs would be reduced.

Applications to Tree Breeding

Data resulting from this study are generally applicable to the breeding of improved strains of longleaf pine. Most obvious is their use as guides to adoption or rejection of traits to be used in selection for specific breeding objectives. In addition, the correlations between traits afford estimates which can be used to select or reject traits for their secondary effects. Thus, dormant season bud length, which was highly correlated with survival, may be useful in selection to minimize mortality. On the other hand, the high correlation of taper factor with basal area should obviate any necessity for separate selection for taper where the major breeding objective is maximum volume.

Of special import is the light thrown on the contribution of parent diameter (basal area) to selection for maximum growth. The chief constituents of volume are height and diameter. In this experiment, parent diameters were not correlated with those of progeny, but the correlation for height/age factor showed that height/age was inherited. In another study of longleaf pine (Snyder 1969) similar relationships were found. Therefore, selecting for diameter or selecting for volume, which is calculated from diameter, introduces considerable error compared to selection only for the heritable trait, height/age ratio. Also, in the current study, diameter growth was one of two traits whose parent-progeny correlation was not proportion to the sib-heritability. Apparently, diameter of individual parent trees in variable wild stands is so modified by stand density and other conditions that genetic variation is obscured. Thus, in selecting longleaf pine parents in open wild stands with variable stand densities, reliance should be placed on height alone. This advice would not be true, however, if parents are to be selected from uniformly managed plantations. Also, in the progeny test diameter growth was as important a constituent of volume as was height; hence it should be retained as a criterion for family selection.

Genetic correlations of volume with foliage weight (0.84) and with branch length/bole height (0.84) indicate that these characters could be used indirectly to improve volume. Selection for small diameter branches would result in increased volume growth, but selection for shorter or fewer branches would have the opposite effect. Some

of these correlations would make crown efficiency selection difficult.

General Combining Ability correlations between open- and cross-pollinated progeny suggest an opportunity for time and cost savings by using open-pollinated progeny tests. These correlations ranged from 0.2 to 0.9 and were proportional to sib-heritability values. Families were ranked about the same by data from either cross- or open-pollinated progeny. Since OP progeny can be obtained with much less cost and effort, their use in first generation testing can expedite results and lower costs. For second generation breeding stock, however, the more expensive cross-pollinations may be necessary to insure maximum gains.

Reliability of seedling measurements as predictors of future longleaf pine height growth were questioned by Wakeley (1971) because he found that some seedlings do not maintain their early height rank. He suggested delaying selection until progeny are 20 years old. In the current study, genetic correlation between 3- and 7-year heights was 0.9, and there were moderate correlations between parent and juvenile heights. These are consistent with similar findings reported by Snyder (1969, 1973) and with progeny height gains from parents selected as juveniles reported by Snyder and Derr (1972). These correlations appear strong enough to justify some parental selection from among trees with good height growth, and justify intensive early selection of families on the basis of progeny heights. If slow-growing families later show superior growth, they can be reintroduced into the breeding program.

Results of our study confirm that there would be gains in form as well as volume growth if, as recommended by some geneticists, longleaf pine seed orchards were established from untested plus trees and later rogued after progeny testing. The current study and Snyder's previous work (1969, 1973), however, suggest a different strategy for breeding improved longleaf pine. Many more parents than needed for the seed orchard would be selected from those with the best height/age ratios. Open-pollinated progeny of these candidate parent trees would be evaluated when the best families have started height growth (5 years or less). In the meantime, ortets would be protected and if necessary grafted. Only after this progeny test would the seed orchard be made up from the qualifying elite parents. This procedure is a notable exception to the concept of using

untested clonal orchards (Namkoong 1970). The increased number of potential parents to be tested reflects the fact that while height growth rates of parents and progeny are related, the truly superior parents are not confined to the phenotypes with the highest growth rates. Testing with open-pollinated rather than the much more expensive cross-pollinated progeny should provide information on enough trees to greatly improve the chance of including the truly outstanding genotypes. Such a program involves perhaps 5 years' delay in quantity production of first generation superior seed. Gains when available, however, should exceed first generation gains from seed orchards established prior to progeny testing.

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To receive a copy of the chart containing the study results, contact the Southern Research Station 200 W. T. Weaver Blvd., Asheville, NC 28804 Phone: 828/257-4830 or send an e-mail to:

pubrequest@srs.fs.usda.gov

Seven-year-old progeny from crosses among 13 randomly se-
lected parent trees provided genetic information on 51 growth,
form, foliage, branch, bud, and pest resistance traits. Presented
are heritabilities, phenotypic and genotypic variances, covari-
ances, General Combing Ability (GCA), Specific Combining
Ability (SCA), and environmental correlations for all measured
traits. The results were compared to those from wind pollina-
tions and to parent-tree measurements where appropriate.